

# CYTOLOGY AND SYSTEMATICS OF THE *MORAEA FUGAX* COMPLEX (IRIDACEAE)<sup>1</sup>

PETER GOLDBLATT<sup>2</sup>

## ABSTRACT

The *Moraea fugax* complex, widespread in the winter rainfall area of southern Africa, is treated here as comprising three species, *M. gracilenta* and the new *M. macrocarpa*, both of restricted distribution and morphologically and cytologically uniform, and the very widespread and variable *M. fugax*. The latter comprises two subspecies: larger flowered populations of robust plants with large capsules and one or two channeled leaves are referred to subsp. *fugax* while small-flowered forms with small capsules and usually two filiform leaves are referred to subsp. *filicaulis*. Cytologically *M. fugax* is remarkably variable. Basic chromosome number in *Moraea* and in the complex is  $x = 10$ , and  $n = 10$  is the only number known for *M. gracilenta* and *M. macrocarpa*. *Moraea fugax* subsp. *fugax* has a base number of  $x = 10$  but exhibits an extensive aneuploid series with populations or races having  $n = 9, 8, 7, 6$ , and  $5$ . Subspecies *filicaulis* has haploid numbers of  $n = 9, 6$ , and  $5$ , the former perhaps basic for this taxon. Some correlation of morphological and karyotypic variation suggests that aneuploid decrease occurred in several morphological lines as geographical races differentiated from the ancestral stock during alternating dry and wet phases of the Quarternary. A revised classification of the complex is presented in the second half of the paper, following a detailed description of the karyological and morphological variation. The karyology of *M. fugax* is not completely known, but the major features are probably reflected in the data presented here.

The *Moraea fugax* complex (*Moraea* sect. *Subracemosae* sensu Goldblatt, 1976a) is one of the most taxonomically complex groups in this pan African genus of some 120 species. *Moraea fugax* is the major taxon of the section with one or more distinctive segregates sometimes recognized as varieties or separate species. The section has been variously treated in the past as comprising one species and four varieties as in "Flora Capensis" (Baker, 1896) or as three species (Baker had added two new species to the complex by 1906). In the most recent revision of *Moraea* in the winter rainfall area of southern Africa, only two species (Goldblatt, 1976b) were recognized, the uniform and local *M. gracilenta* Goldbl. and the widespread and variable *M. fugax* (de la Roche) Jacq. [(= *M. edulis* (L. f.) Ker]. The complex is distinctive in its vegetative habit. The branches are short and often clustered in a semi-umbellate manner, and the one or two foliage leaves are inserted near the stem apex at the point of branching, usually well above the ground. The flowers are of the basic type for the genus with large outer tepals marked with nectar guides, smaller inner tepals, and large flattened style

branches with well-developed crests, but the capsules are distinctive in having a well-developed beak. Morphological variation is extensive and confusing. Several races can be distinguished in *M. fugax* but the existence of many intermediates has made recognition of additional species or subspecies difficult and impractical.

Since my revision I have had the opportunity to observe and collect members of the complex extensively in the field. As a result I have a deeper understanding of the patterns of morphological variation and have assembled considerably more cytological data. This new information has made a review of the complex necessary. I now recognize three species in the complex: *M. gracilenta*; the new *M. macrocarpa*, comprising dwarf, blue-flowered and often unbranched plants with long capsules and nearly sessile spathes; and *M. fugax* with two subspecies, *filicaulis* (Baker) Goldbl., including dwarf plants with small, white to cream or rarely blue flowers, small capsules, and stalked spathes, and subsp. *fugax* for larger flowered, robust plants with either white, blue, or yellow flowers and large capsules. Along the west coast several races or forms of subsp. *fugax*

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<sup>2</sup> B. A. Krukoff Curator of African Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166.



TABLE 1. Chromosome number and collection information for previously published and original counts presented in this paper for *Moraea* sect. *Subracemosae*. Original counts are in bold print.

Species	Diploid Number (2n)	Collection Data
<i>M. gracilenta</i>	20	below Piekenierskloof Pass, <i>Goldblatt</i> 3279 (MO).
	<b>20</b>	riverside, Clanwilliam campsite, <i>Goldblatt s.n.</i>
<i>M. macrocarpa</i>	<b>20</b>	mountains W of Trawal, <i>Goldblatt</i> 5661 (MO); farm Reiers Rus near Worcester, <i>Goldblatt &amp; Snijman</i> 6961 (MO); near Piketberg, <i>Anon s.n.</i> ex hort. Kirstenbosch.
<i>M. fugax</i> subsp. <i>fugax</i>	<b>20</b>	Olifants River Bridge, near Klawer, <i>Goldblatt</i> 2828 (MO); mountains W of Trawal, <i>Goldblatt</i> 5667 (MO); NW of Nieuwoudtville, <i>Goldblatt</i> 5843 (MO).
	<b>18</b>	near Wallekraal, Namaqualand, <i>Goldblatt s.n.</i> no voucher; Bokbaai road, <i>Goldblatt</i> 5850 (MO); Donkergat Peninsula, <i>Goldblatt s.n.</i> no voucher; near Robertson, <i>Goldblatt</i> 5860 (MO); near Brandewyn River, <i>Goldblatt</i> 4812 (MO); Cedarberg at Algeria, <i>Viviers s.n.</i> (MO); farm Reiers Rus near Worcester, <i>Goldblatt &amp; Snijman</i> 6962 (MO).
	16	8 km N of Malmesbury, <i>Goldblatt</i> 3025 (MO).
	<b>16</b>	commonage at Malmesbury, <i>Goldblatt</i> 4813 (MO); 20 km NW of Malmesbury, <i>Goldblatt</i> 4081 (MO); sandy soil at Klawer, <i>Goldblatt</i> 5662 (MO); Pakhuis Pass near Leipoldts Grave, <i>Goldblatt s.n.</i> (MO).
	<b>14</b>	Cape Point Reserve, <i>Goldblatt</i> 5403 (MO); Caledon Zwartberg, Swarttrivier, <i>Goldblatt</i> 5782 (MO); near Velddrif, sandy plains, <i>Goldblatt s.n.</i> (MO).
	12	Hopefield, <i>Goldblatt</i> 152 (J).
	<b>12</b>	foot of the Elandskloof Mts., Elandsberg farm, <i>Goldblatt</i> 5851 (MO); near Bellville, <i>Delpierre s.n.</i> no voucher; Silvermine, Cape Peninsula, <i>Goldblatt</i> 5164 (MO).
	<b>10</b>	(cytotype A, southwestern Cape populations): Malmesbury, near Abbotsdale, <i>Goldblatt</i> 5116 (MO); foot of Houw Hoek Pass, <i>Goldblatt</i> 4292 (MO); slopes of Koeberg, N of Cape Town, <i>Goldblatt</i> 4080 (MO); Kommetje, Cape Peninsula, <i>Goldblatt s.n.</i> no voucher; Paarl flats, <i>Goldblatt s.n.</i> no voucher; Cape Peninsula, foot of Klaasjagersberg, <i>Goldblatt</i> 5264 (MO).
		(cytotype B, Olifants River Valley populations): foot of the Winterhoekberg N of Klawer, <i>Goldblatt</i> 5778 (MO); Olifants River Valley, near Clanwilliam, <i>Goldblatt</i> 5936 (MO).
<i>M. fugax</i> subsp. <i>filicaulis</i>	<b>18</b>	Ramskop, Clanwilliam, <i>Goldblatt</i> 7376 (MO).
	12	Gifberg slopes, <i>Goldblatt</i> 207 (BOL).
	<b>12</b>	granite hills near Kamieskroon, <i>Goldblatt</i> 4254 (MO); Kamiesberg, Rooiberg slopes, <i>Goldblatt</i> 4308 (MO); Richtersveld, Eksteenfontein road, <i>Goldblatt</i> 5717 (MO).
	<b>10</b>	flats below Wildeperdehoek Pass, <i>Goldblatt</i> 5761 (MO); hills W of Trawal, Kleipan road, <i>Goldblatt</i> 5666 (MO).

can be recognized, each distinguished by small differences in morphology such as flower color, vegetative size, leaf number, and occasionally in the relative proportions of floral parts. The different races displace one another either geographically in suitable habitats or less often temporally. Where subsp. *fugax* is sometimes sympatric with subsp. *filicaulis* or *M. macrocarpa* it usually flowers at the same time, but no hybrids or intermediates are known.

Until now chromosome information for the complex has been limited (Goldblatt, 1971,

1976a, 1976b). *Moraea gracilenta* was reported to have a diploid number of  $2n = 20$ , and  $x = 10$  is presumably basic for the complex. But  $2n = 16$  was recorded in one population of *M. fugax* and  $2n = 12$  in two others, one a large white-flowered form and the other corresponding to the dwarf and slender stemmed *M. filicaulis* Baker. Numerous chromosome counts are now available (Table 1). New data indicate that *Moraea gracilenta* and *M. macrocarpa* are cytologically uniform ( $2n = 20$ ), but the more widespread *M. fugax* now appears remarkably variable



chromosomally. Chromosome numbers range from  $2n = 20$  to  $2n = 10$  in subsp. *fugax* and  $2n = 18, 12$ , and  $10$  in subsp. *filicaulis*. Variation in the karyotype is correspondingly extensive, and karyotypes range from predominantly acrocentric complements with  $2n = 20$  or  $18$  and medium to small chromosomes, to those with  $2n = 16, 14, 12$ , or  $10$  and one to three large metacentric pairs and much smaller acrocentrics. The total amount of chromosome material seems fairly constant (Table 2) in all karyotypes, based on a comparison of total chromosome length. Polyploidy has played no role in numerical changes in the complex that thus stands out as a group where aneuploidy alone has apparently resulted in the extreme karyotypic variability.

RELATIONSHIPS

The complex, as sect. *Subracemosae*, was assigned to subg. *Moraea* (Goldblatt, 1976a) largely because of its generalized flower and basic chromosome number,  $x = 10$ , which corresponds to the base number for the genus. It is apparently allied to sect. *Deserticola* (five species), which occurs in the drier parts of the Cape west coast and in southern Namibia. The species of sect. *Deserticola* all have a basal or nearly basal leaf and an open branching system but resemble sect. *Subracemosae* in the tendency to develop a short beak on the capsule, especially *M. macgregorii* Goldbl.

GEOGRAPHICAL DISTRIBUTION

The section is restricted to the winter rainfall region of southern Africa and extends along the west coast from just south of the Orange River to Knysna on the south coast (Fig. 1), a distance of some 900 km. *Moraea gracilenta* has a limited range at the foot of the mountains and intermontane valleys from Tulbagh to Clanwilliam in the Olifants River Valley. *Moraea macrocarpa* is equally restricted in its range and occurs in deep, coarse sand mainly on the west coast from Saldanha to Clanwilliam but also in the Breede River Valley near Worcester. *Moraea fugax* is found throughout the range of the section. Records are few and scattered east of the Caledon and Worcester districts but *M. fugax* has been collected at Knysna on the south coast some 400 km east of Cape Town and has even been reported from Humansdorp (Moriarty, 1982), but specimens are needed to confirm this. The complex is clearly infrequent east of Caledon and

TABLE 2. Mean total length of the chromosome complement in selected populations of *Moraea fugax* and *M. gracilenta*.

Species	Length (cm)	Length (μm)
<i>M. gracilenta</i>		
$2n = 10$ (Clanwilliam)	19.4	87.4
<i>M. fugax</i> subsp. <i>fugax</i>		
Large white-flowered form		
$2n = 20$ (Klawer)	23.2	104.5
$2n = 20$ (Trawal)	21.8	90.2
$2n = 18$ (Donkergat)	19.1	86
$2n = 14$ (Velddrif)	20.8	93.6
Late-blooming blue-flowered form		
$2n = 12$ (Silvermine)	23.6	106.2
Large yellow-flowered form		
$2n = 10$ (Houw Hoek)	22.4	100.9
<i>M. fugax</i> subsp. <i>filicaulis</i>		
$2n = 12$ (Kamieskroon)	19.8	88.9

evidently less variable there. Subspecies *filicaulis* is common in Namaqualand, but it extends south along the west coast into the Olifants River Valley south to Clanwilliam. Its range overlaps that of subsp. *fugax* and the two are sympatric at several localities.

METHODS

CYTOLOGY

All chromosome observations were made at mitotic metaphase in root tip squashes. Root tips from either sprouting corms or germinating seeds were harvested in midmorning and pretreated in 8-hydroxyquinoline at refrigerator temperatures for seven to eight hours, before fixation in ethanol-acetic acid (3 : 1) for two to three minutes. The tips were then either stored in 70% ethanol or immediately hydrolyzed in 10% HCl for six minutes before being transferred to water. Root tip apices were squashed in lacto-propionic orcein (Dyer, 1963) or FLP orcein (Jackson, 1975). With few exceptions, the plants used in the study were collected in the wild by myself (Table 1), and voucher specimens were made for plants in suitable condition. Unvouchered accessions will be grown, wherever possible, to flowering and then pressed. Vouchers have been placed in the Missouri Botanical Garden Herbarium (MO). The method used here differs from that employed previously (Goldblatt, 1971, 1976a) in



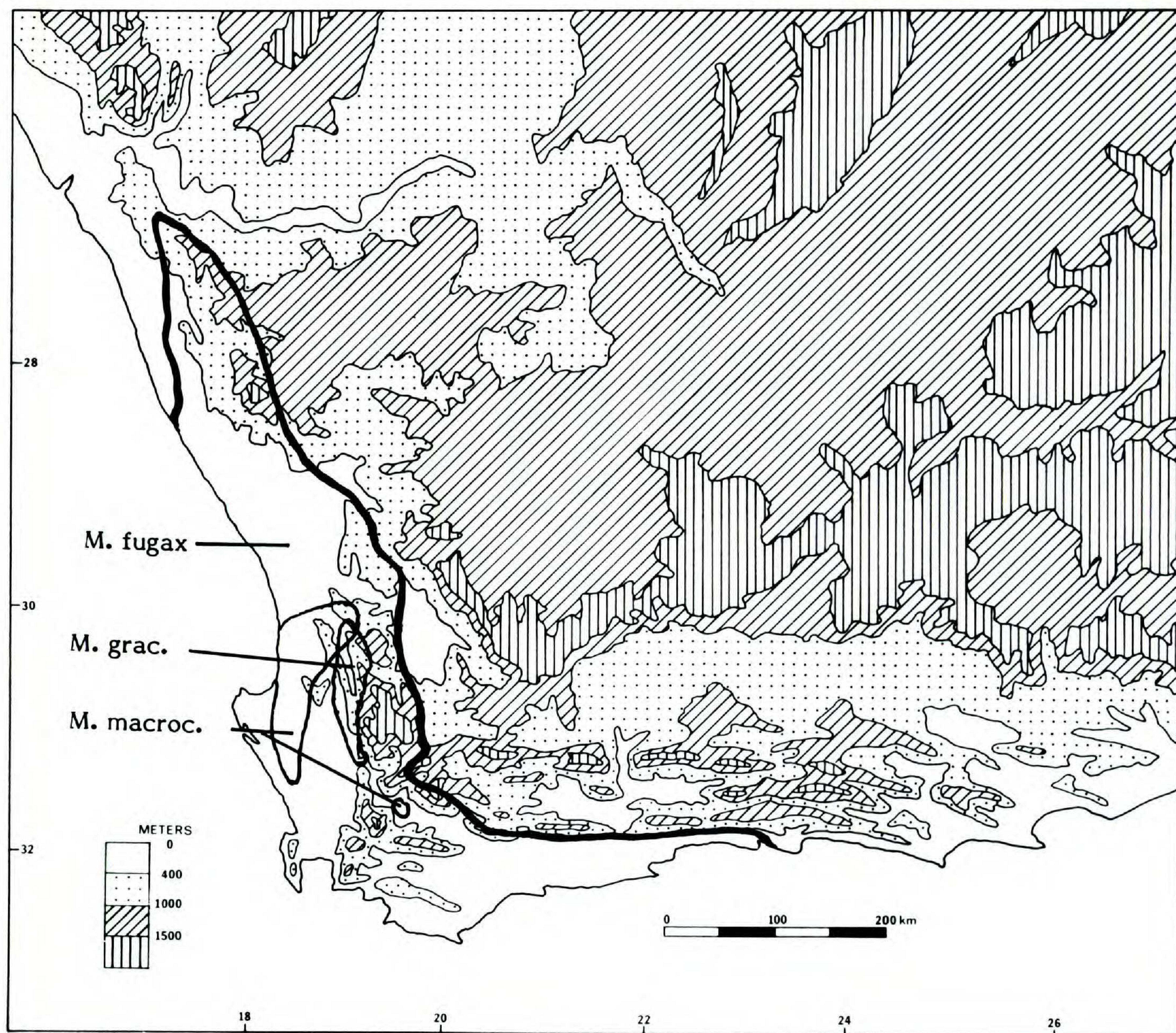


FIGURE 1. Geographical distribution of *Moraea fugax*, *M. gracilenta*, and *M. macrocarpa*.

my studies of *Moraea* cytology, so that measurements are not directly comparable. All figured metaphases are drawn at the same scale. Metaphases selected for illustration are representative of a particular population or karyotype group (Figs. 2, 4, 5). Minor differences between karyotypes of different populations have not been figured for reasons of economy of space, and while these differences may be significant, they are not of the same magnitude as those dealt with here.

#### TAXONOMY

Live material of all species and numerous populations was examined before preservation, and illustrations were made from living plants. Specimens from the herbaria with important southern African collections were also studied. Measurements were made from live plants when possible but also include the variation found in

dry material, in which the delicate parts of the flowers shrink some 10–15%. Flower color fades progressively in dry specimens, eventually changing completely, sometimes becoming darker and usually disappearing. Color notes on collected specimens are desirable and are frequently mentioned by collectors.

Material examined is cited according to the grid reference system based on geographical degree co-ordinates of latitude and longitude in current use in southern Africa (Edwards & Leistner, 1971).

#### KARYOTYPES

A chromosome number of  $2n = 2x = 20$  occurs in *Moraea macrocarpa*, *M. fugax* subsp. *fugax*, and *M. gracilenta*, and I believe it is basic for *Moraea* and for the complex. *Moraea fugax* subsp. *fugax* is cytologically heterogeneous and



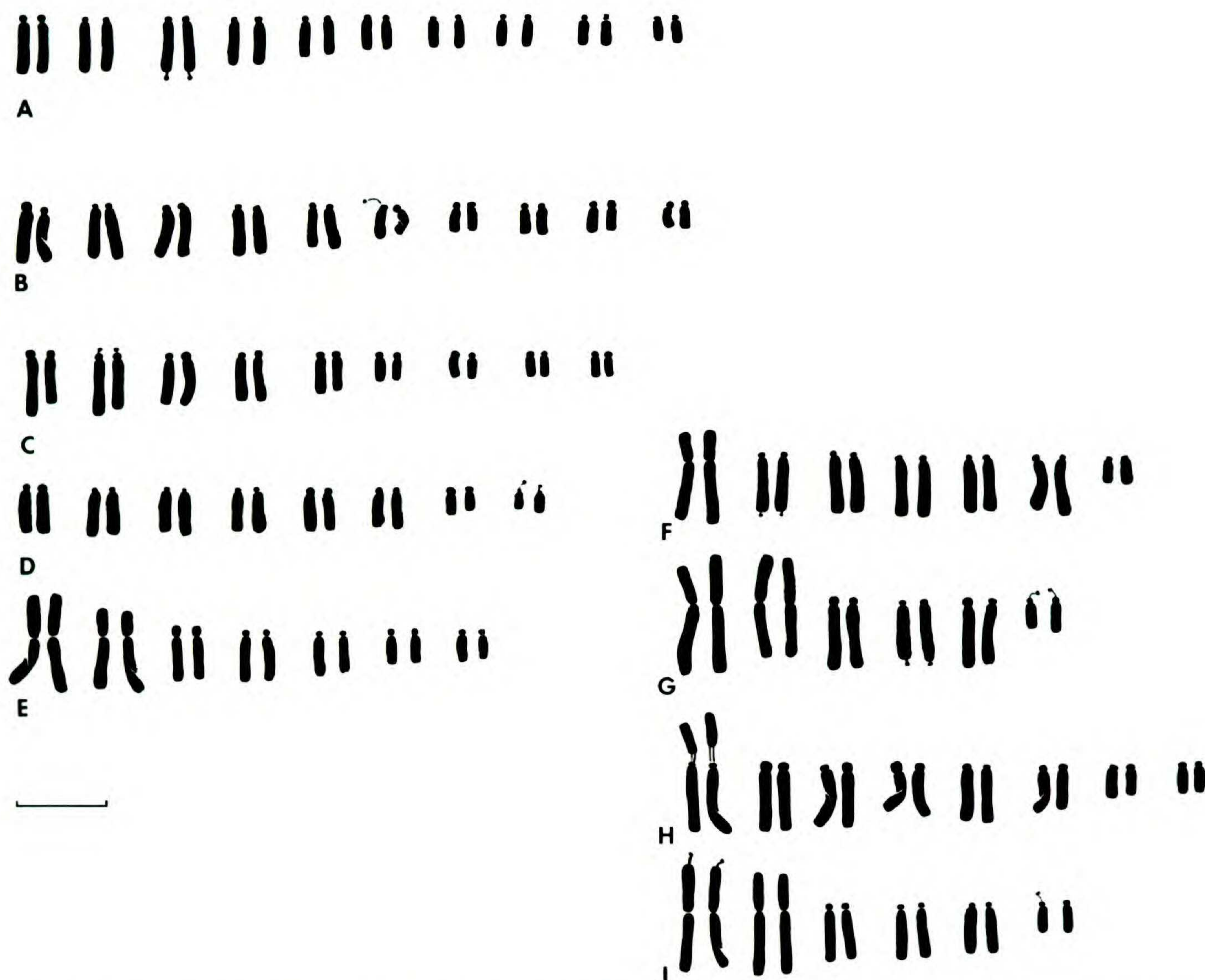


FIGURE 2. Chromosome cytology of the *Moraea fugax* complex. —A. Mitotic chromosomes of *M. macrocarpa*,  $n = 10$ . B–I. *Moraea fugax* subsp. *fugax*. B–E. Large white-(pink-)flowered form. —B. Kleipan road near Trawal,  $n = 10$ . —C. Donkergat Peninsula,  $n = 9$ . —D. Near Klawer,  $n = 8$ . —E. Velddrif road,  $n = 7$ . F, G. Blue-purple-flowered form. —F. Cape Point,  $n = 7$ . —G. Silvermine, Cape Peninsula,  $n = 6$ . H, I. Small white-flowered form. —H. Malmesbury,  $n = 8$ . —I. Near Gouda,  $n = 6$ . Scale = 10  $\mu\text{m}$ .

also has  $2n = 18, 16, 14, 12$ , and 10 (Figs. 2, 4). *Moraea fugax* subsp. *filicaulis* has  $2n = 18, 12$ , and 10 (Fig. 5). Karyotypes vary considerably but are usually similar for each diploid number. They are briefly described in the following paragraphs. Voucher data and chromosome number for all populations examined are presented in Table 2.

*MORAEA GRACILENTA*, *M. MACROCARPA* & *M. FUGAX*  
SUBSP. *FUGAX*  $2n = 20$  CYTOTYPE

Eight populations, including two of *Moraea gracilentata*, three of *M. macrocarpa* (Fig. 2A), and three of *M. fugax* (Fig. 2B), have  $2n = 20$  and similar karyotypes with strongly acrocentric chromosome pairs. Variation in chromosome length is appreciable, the longest being about twice the shortest. Four to five large chromosome pairs

(7–8  $\mu\text{m}$  long), one to two medium pairs, and four (or five) short pairs (3–4  $\mu\text{m}$  long) can be recognized. Satellites, not consistently observed, are on a short pair.

*MORAEA FUGAX* SUBSP. *FUGAX*  
 $2n = 18, 16, 14$  & 12 CYTOTYPES

1.  $2n = 18$  karyotypes (tall white- and smaller yellow-flowered forms). The seven populations of *Moraea fugax* subsp. *fugax* with  $2n = 18$  have karyotypes similar to those with  $2n = 20$ . There are five long and four short pairs of acrocentric chromosomes. One individual of a population from Donkergat Peninsula (*Goldblatt s.n.*) is structurally heterozygous with 11 long and seven short chromosomes. Two other individuals of the population had ten long and eight short chromosomes. Satellites were seen clearly only in the



Donkergat population on the short arms of a long chromosome pair (Fig. 2C).

2.  $2n = 16$  karyotypes (white- and pink-flowered forms). Five populations have  $2n = 16$ . Three of these are a distinctive white-flowered form with narrow tepals from the Malmesbury area. The karyotype of this form (Goldblatt, 1976a; Fig. 1G) comprises a long acrocentric pair with conspicuously large satellites, four only slightly shorter acrocentric pairs, and three short acrocentric pairs (Fig. 2H). Another population matching this form has  $2n = 12$  (Fig. 2I) (see below).

A second karyotype, with  $2n = 16$ , was found in a single unusual, pale pink-flowered population from the Olifants River Valley (Goldblatt 5662) and consists of six medium to long acrocentric and two short acrocentric pairs, one of which has small satellites (Fig. 2D). This karyotype is quite different from the white-flowered Malmesbury form with  $2n = 16$  and must be of independent origin.

A yellow-flowered population from Pakhuis Pass also has  $n = 16$  (Fig. 4A). The karyotype comprises one long submetacentric pair, and the remainder are strongly acrocentric. One of the longer of these pairs has a small satellite located at the end of a long arm, a feature of most populations of yellow-flowered plants studied.

3.  $2n = 14$  karyotypes (white, yellow, or blue forms). Three populations, each morphologically distinct, have  $2n = 14$ . One of these, a large yellow-flowered form from Caledon Zwartberg (Goldblatt 5782), has one pair of large metacentrics (16  $\mu\text{m}$  long), five medium-sized pairs (8–10  $\mu\text{m}$  long) two of which are acrocentric, two telocentric, one metacentric, and a tiny acrocentric pair (Fig. 4B). There are satellites on one of the telocentrics. Other plants matching this relatively short-stemmed but large yellow-flowered form have  $2n = 10$  and three large metacentric chromosome pairs.

A second population with  $2n = 14$  is a blue-flowered and late-blooming form from the Cape Peninsula. The karyotype comprises a long submetacentric pair, ten strongly acrocentric medium-sized pairs, and one very short acrocentric pair (Fig. 2F). Satellites were not readily seen but appeared to be on the long arm of one of the medium-sized acrocentric pairs. Other populations of this form have  $2n = 12$ , and their karyotypes differ by a very long metacentric pair.

The third population with  $2n = 14$  was collected near Velddrif on the west coast and had

large white flowers. The karyotype comprises a long metacentric pair, two long and one medium pair, and two short pairs (Fig. 2F). Most populations of this tall white-flowered form have  $2n = 20$  or 18, but  $2n = 12$  has been recorded from one locality (Goldblatt, 1971).

4.  $2n = 12$  karyotypes (large white- or blue-flowered forms). Four populations have  $2n = 12$ . Three of these, all from the southwest Cape, represent the large blue- (to white-) flowered and moderately robust late-blooming form common in sandy soils. The karyotype (Goldblatt, 1971) is similar in all populations. There are two long metacentric pairs, three medium-sized acrocentrics, and a tiny acrocentric pair (Fig. 2G). Satellites were seen occasionally on the longest and shortest pairs. A white-flowered population from near Gouda (Goldblatt 5851) has a similar karyotype (Fig. 2I), but the plants are apparently identical with the slender white-flowered form with narrow tepals from the Malmesbury area having  $2n = 16$ .

5.  $2n = 10$  karyotypes (large yellow-flowered forms). Of the eight populations with  $2n = 10$ , six represent the large yellow-flowered, typical form of *Moraea fugax* from the southwestern Cape. The karyotype (Fig. 4C) consists of two metacentric pairs 13–14  $\mu\text{m}$  long, one submetacentric 12–13  $\mu\text{m}$  long, and two much shorter acrocentrics 7–8  $\mu\text{m}$  long. Satellites are on the end of the long arm of a short pair and the longest of the two metacentric pairs.

The second karyotype of subsp. *fugax* with  $2n = 10$  occurs in yellow-flowered populations in the Olifants River Valley (Fig. 4D). It comprises two long metacentrics, a medium-sized meta- to submetacentric, a medium-sized acrocentric, and a pair of tiny subtelocentrics with large satellites. A second pair of satellites was seen, in one population (Goldblatt 5778), on the longer arm of the longest metacentric pair. These populations are notable in having nearly erect inner tepals, and they differ from the southern yellow-flowered form in this feature as well as in details of their karyotype.

#### *MORAEA FUGAX* SUBSP. *FILICAULIS*

Only one population of subsp. *filicaulis* has so far been found, with  $2n = 18$ , from Clanwilliam in the far south of its range. This karyotype comprises ten long and eight short chromosomes, all strongly acrocentric. Two central Namaqualand populations have  $2n = 12$ . One of these is a small,



TABLE 3. Comparison of some critical morphological characteristics of the species of *Moraea* sect. *Subracemosae*. Color key: bl = blue; ye = yellow; wh = white.

Species	Branches	Spathes (cm)	Outer Tepal (cm)	Capsule (mm)	Anther (mm)	Color
<i>M. gracilentata</i>	many, open	2.5–3.5	2–2.6(–3)	8–12	4–6.5	bl
<i>M. macrocarpa</i>	few, sessile	4–5(–6.5)	2–3	(18–)20–25	4–5	bl
<i>M. fugax</i> subsp. <i>filicaulis</i>	several, usually congested	2–3.5(–4)	2–2.6(–3.1)	9–13(–15)	4–5(–6)	bl, wh
<i>M. fugax</i> subsp. <i>fugax</i>	several, usually congested	(3.5–)4–6	2.7–4	15–22	5–10	bl, wh, ye

dark blue-violet-flowered form that corresponds to the type of Baker’s *M. filicaulis*. The other population has white flowers. The karyotype consists of two pairs of long acrocentrics and a graded series of smaller acrocentrics (Fig. 5A). There are very large satellites on the short arm of one of the longest pairs.

A population from the southern Richtersveld, in the extreme north of the range of *Moraea fugax*, also has  $2n = 12$  but has a different karyotype (Fig. 5B) comprising a long metacentric pair, a fairly long submetacentric (-acrocentric) pair, three medium-sized acrocentric pairs, and an unusual small metacentric pair. Small satellites are on the long arms of a medium-sized chromosome pair. This is somewhat similar to karyotypes in the two populations with  $2n = 10$ , which have one long metacentric and four medium-sized acrocentric pairs and lack the short metacentric pair (Fig. 5C). The populations with  $2n = 10$  are from opposite ends of the range of subsp. *filicaulis*, from the lower Olifants River Valley (Goldblatt 5666) and from northern Namaqualand (Goldblatt 5761). Satellites, seen only in the latter population, are located on the metacentric pair.

The karyotype previously published for subsp. *filicaulis* (Goldblatt, 1971: 348), also  $2n = 12$ , corresponds to none of those described above. It has one large metacentric pair, four submetacentric pairs, and an acrocentric pair. The highest number recorded for the subspecies is presumed to be basic,  $x = 9$ .

MORPHOLOGY

PATTERNS OF VARIATION

The characters that unite the taxa of the *Moraea fugax* complex are: (1) the tendency for the branches to be clustered at the insertion of the leaf or leaves due to the typically short internodes above the leaves, (2) the elongate basal internode

so that the leaf is usually inserted well above ground, and (3) a strongly beaked capsule.

In *Moraea gracilentata* the branches form an open system, and in *M. macrocarpa* the stem is often very short and reaches only shortly above ground level at flowering time, elongating somewhat in fruit.

Excluding the peculiarities noted above for *Moraea gracilentata* and *M. macrocarpa*, variation within the section is largely restricted to size, relative proportion of characters (Table 3), and flower color, discussed further below. The tendency for production of either one or two leaves is conspicuous in *M. fugax*. Plants from most populations of subsp. *filicaulis* have two filiform leaves. Some white-flowered populations of subsp. *fugax* have either one or two equal or unequal, linear, channeled leaves.

Plant and flower size, and color are particularly variable in *M. fugax*, and the variation is sometimes correlated with chromosome variation. Races are not sufficiently separable on either morphological or cytological grounds to make an extensive infraspecific classification desirable, and only the consistently smaller Namaqualand and northwest Cape forms with  $2n = 18, 12$ , or  $10$  seem to merit subspecific recognition. Even in this subspecies the degree of chromosomal variation is unusual, and five of the six populations studied can be distinguished by major differences in their karyotypes. Nevertheless, these populations probably have a common ancestry and merit taxonomic recognition.

*Plant size.* Populations fall roughly into two categories (Table 3): either robust and large-flowered with spathes (3.5–)4–6 cm long and outer tepals 2.7–4 cm long (only forms of subsp. *fugax*) or dwarf and small-flowered spathes 2–3.5(–4) cm long and outer tepals 2–2.6(–3.1) cm long. Flower and spathe size are good indications of overall plant size, because most other characters are similarly proportioned. *Moraea gracilentata* is







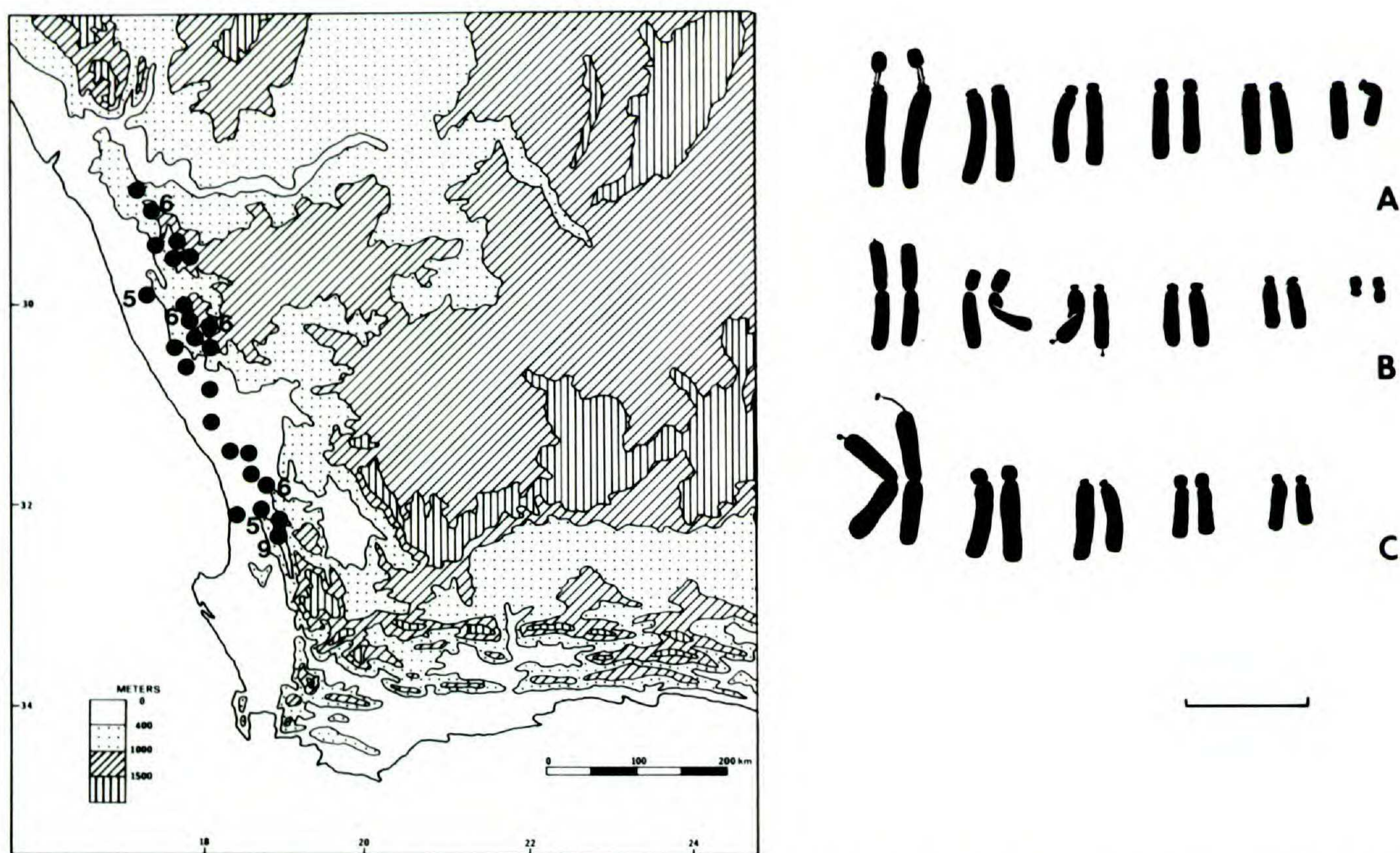


FIGURE 5. Mitotic chromosomes and geographical distribution of *Moraea fugax* subsp. *filicaulis*.—A. Near Kamieskroon,  $n = 6$ .—B. Eksteenfontein road, Richtersveld,  $n = 6$ .—C. Below Wildepaardehoek Pass,  $n = 5$ . Haploid numbers are indicated for populations where known. Scale = 10  $\mu\text{m}$ .

reason for treating them as subspecies rather than as separate species. In some instances determinations may be arbitrary either because the plants in question are poorly grown or poorly pressed, or the plants may be truly intermediate in more than one characteristic.

**Flower color.** Blue-purple flowers are characteristic of all populations of *M. gracilentia* and *M. macrocarpa* but are less common in *Moraea fugax*. In the Kamiesberg, populations of subsp. *filicaulis* (corresponding exactly to the type of *M. filicaulis*) have deep blue-purple flowers, but elsewhere the subspecies has white to cream flowers, sometimes flushed pink or yellow. In subsp. *fugax*, blue to purple flowers occur in the Piketberg area and from Malmesbury south to the Cape Peninsula where they bloom later than yellow- or white-flowered populations. Chromosome numbers in this form are  $n = 6$  and  $n = 7$  (Fig. 2F, G), the latter found in only one population.

White-flowered populations of subsp. *fugax* are most common along the west coast (Fig. 3) and extend from just north of the Cape Peninsula to northern Namaqualand. Chromosome numbers are  $n = 10$ , 9, 7, and 6, the latter two numbers infrequent. In the Olifants River Valley, white-flowered populations alternate with yellow-flowered populations, the latter consistently differing

in having erect inner tepals (and  $n = 5$ ). Occasionally there is a trend for white flowers to be replaced gradually over some distance by blue ones. Populations with smaller white flowers and narrow tepals occur in the Malmesbury district and in the Breede River Valley (Fig. 3). These have  $n = 9$ , 8, or 6. They appear to comprise a separate white-flowered race in which aneuploid reduction has occurred independently.

Yellow-flowered forms are most common in the southwestern Cape where the type of *Moraea fugax*, an illustration of a plant of unknown origin, was most probably collected. This southern form has  $n = 5$  over much of its area (Fig. 4), but  $n = 7$  is known from one population. Yellow-flowered plants in the Olifants River Valley also have  $n = 5$  but have a somewhat different karyotype with the smallest chromosome pair minute and metacentric (Fig. 4D). In some of the interior mountain valleys of the western Cape, from Pakhuis Pass to Robertson, similar but more slender yellow-flowered plants have either  $n = 9$  or 8. Despite the several different karyotypes found in plants with yellow flowers, there seems to be no consistent and significant morphological feature to distinguish them. It is not clear whether the karyotypically diverse yellow-flowered forms comprise a monophyletic assemblage or evolved



more than once from ancestors that most probably had white flowers.

### EVOLUTION

The cytological diversity in *Moraea* sect. *Subracemosae* is certainly without parallel in Iridaceae and is most unusual in plants generally. The section appears to be in a stage of rapid evolution with the differentiation of numerous regional and local morphological and cytological races. *Moraea fugax* is the most chromosomally variable and probably also the most morphologically variable species in *Moraea* and its close allies (Goldblatt, 1971, 1979, 1980). Other species, notably *M. tripetala* and *M. papilionacea*, are also morphologically variable and have differentiated into several distinct forms or races. In these species cytological variability is limited, as would normally be expected, although different cytotypes can be distinguished (Goldblatt, in prep.).

The chromosomal diversity in the several races of *Moraea fugax* probably has promoted population differentiation in the species by restricting hybridization and consequent recombination in forms that have differentiated cytologically. It probably played little role in the origin of population differences that most likely developed in isolation at times when more arid conditions prevailed along the Cape west coast, and the distribution of the various forms or races of the species was more restricted than at present.

It is especially remarkable that the extensive chromosomal variation has developed in several lines. The ancestor of the complex probably had small blue-purple flowers, two long leaves, and many branches in an open arrangement and most likely resembled *M. gracilenta*. This species or its immediate ancestor may have given rise to the dwarf and reduced *M. macrocarpa* and to the larger flowered form of *M. fugax*, both of which have similar karyotypes with  $x = 10$ .

Evolution in *Moraea fugax* presumably followed a pattern of reduction in plant size, length and number of branches, and diversification of flower color. Distinctive forms or races tend to have either fewer branches, shorter stems, or narrower tepals and often have only a single leaf, as in the type form of *M. fugax*.

The evolution of the different color forms in subsp. *fugax* was probably a significant development, although it is difficult to assess its evolutionary importance. The available data do not

favor a single or multiple origin for either blue or yellow color. However, it is clear from the karyology that chromosomal diversification occurred at least once in each of the major color forms after their differentiation. Furthermore, flower color in other species of *Moraea* rarely varies within a species, so it is reasonable to postulate a single (or very few) color change events. Thus it is likely that aneuploid reduction from  $n = 9$  to 5 occurred in a monophyletic yellow-flowered form of subsp. *fugax* and in the late-blooming blue-purple-flowered form at least from  $n = 7$  (the highest number recorded here) to 6. The difference in karyotypes in the yellow-flowered forms with  $n = 5$  from the southwestern Cape and in the Olifants River Valley suggests either an independent origin of this number from a common ancestor with a higher haploid number or major structural change in the karyotype with  $n = 5$ . It also seems likely that plants with smaller white flowers and narrow tepals from the Malmesbury district and Breede River Valley comprise a regional race distinct from the large white-flowered form, and the recorded numbers of  $n = 9$ , 8, and 6 indicate separate aneuploid reduction series in the two white-flowered races.

### SYSTEMATIC TREATMENT

#### KEY TO THE TAXA OF SECTION *SUBRACEMOSAE*

- 1a. Spathes short, 2–3.5(–4) cm long; capsules 8–13 rarely to 15 mm long.
  - 2a. Leaves filiform and usually two; branches few to several clustered; flowers opening shortly after midday ..... 3B. *M. fugax* subsp. *filicaulis*
  - 2b. Leaves linear, usually 2–3 mm wide, solitary; branches many and paniculate; flowers opening after 3:30 P.M. .... 1. *M. gracilenta*
- 1b. Spathes longer, (3.5–)4–6.5 cm long; capsules 15–28(–40) mm long.
  - 3a. Flowers small, the outer tepals 2–3 cm long; capsules at least 18 mm long; branches solitary or two to three and sessile to subsessile ..... 2. *M. macrocarpa*
  - 3b. Flowers large, the outer tepals 2.7–4 cm long; capsules 15–28(–40) mm long; branches usually several and stalked ..... 3A. *M. fugax* subsp. *fugax*

1. ***Moraea gracilenta*** Goldbl., Ann. Missouri Bot. Gard. 63: 724. 1976 [1977]; Fl. Pl. Africa 44: tab. 1748. 1977. TYPE: South Africa. Cape: sandy flats S of Piekenierskloof Pass, Piketberg district, Goldblatt 3279 (holotype, MO; isotypes, K, NBG, PRE, S). FIGURE 6A.



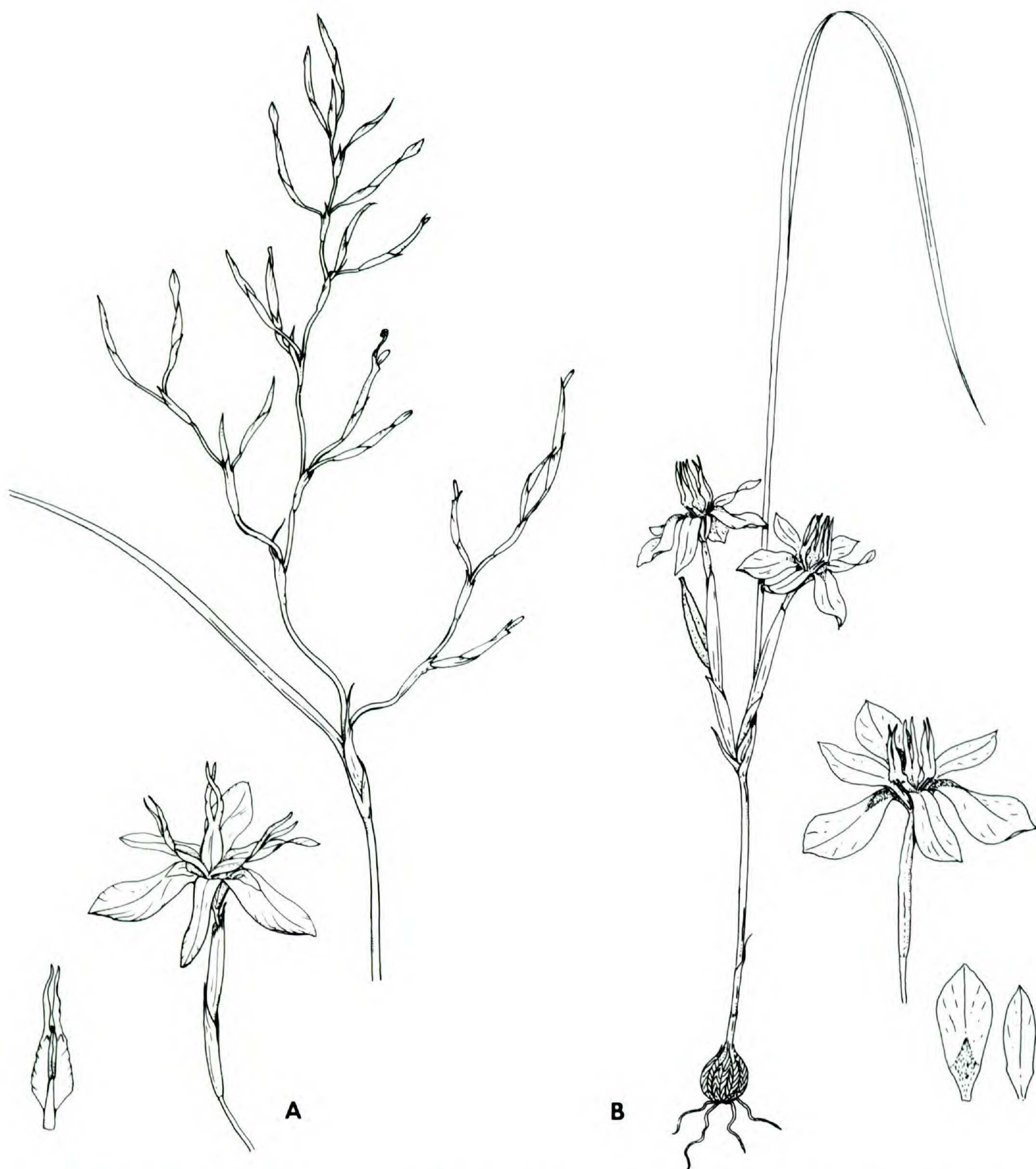


FIGURE 6. Morphology of *Moraea gracilenta* (A) and *M. macrocarpa* (B). Habits  $\times 0.5$ ; flowers, and floral details life size.

*Moraea edulis* L. f. var. *gracilis* Baker, Handb. Irid. 56. 1892; Fl. Cap. 6: 21. 1896. TYPE: South Africa. Cape: Tulbagh Kloof to Piekeniers Kloof, Zeyher 1647 [lectotype, K, designated by Goldblatt (1976b); isoelectotypes, PRE, S].

Plants 30–80 cm high, many branched. *Corm* 1.5–2 cm diam., deeply buried to 25 cm; tunics of fine to medium pale fibers. *Leaf* solitary, canaliculate, linear, exceeding the inflorescence but usually trailing, inserted well above the ground

at the base of the first branch. *Stem* erect and multibranched. *Spathes* herbaceous, becoming dry, the apices brown, acute; inner spathe 2.5–3.5(–4) cm long, the outer less than half the inner. *Flower* pale blue-mauve, strongly scented; *outer tepals* 2–3 cm long, 6–8 mm at the widest point, lanceolate; *inner tepals* 1.8–2.8 cm long, 5–6 mm wide, spreading. *Filaments* ca. 5 mm long, united in the lower half; *anthers* 4–6 mm long, white. *Ovary* 8–10 mm long, included in the spathes, *style branches* 7–9 mm long, crests linear-lan-



ceolate, 7–12 mm long. *Capsule* 8–12 mm long. *Chromosome number*  $2n = 20$ .

*Flowering time.* Late September to November, extending to December at higher altitudes; flowers opening after 3:30 P.M. sometimes as late as 5 P.M. and fading by 7 P.M.

*Distribution.* Western coastal belt from Tulbagh Kloof to Clanwilliam, in sandy flat areas, near streams or at the foot of mountains. Figure 1.

*Moraea gracilenta* differs consistently from all the forms of the variable *M. fugax* in its open and many branched habit, small blue flowers, and short inflorescence spathes and capsules. Its floral phenology is also markedly different from that of *M. fugax*. Blooming occurs in the same months, and the flowers of both species last only a day, but while those of *M. gracilenta* open between 3:30 and 5 P.M. and last until at least 7 P.M., the flowers of *M. fugax* open at about midday and are usually completely wilted by 6 P.M. The difference in phenology has been observed on several occasions in wild populations and appears to vary little. *Moraea gracilenta* is apparently pollinated by small moths, which I have seen visiting the pale, sweetly scented flowers as they open in the late afternoon.

*Specimens examined.* SOUTH AFRICA. CAPE: 32.18 (Clanwilliam) riverbank near Clanwilliam (BB), *Goldblatt* 3076 (MO), *Galpin* 11482 (B, K, PRE); Eendekuil (DB), *Loubser* 851 (NBG); sandy areas between Eendekuil and Piekenierskloof Pass, *Goldblatt* 3279 (K, MO, NBG, PRE, S), 3029 (MO, NBG, PRE).

32.19 (Wuppertal) near Warm Baths, Olifants River Valley (CA), *L. Bolus* s.n. (BOL-20323, K, PRE); Citrusdal, riverbank at campsite, *Goldblatt* 6557 (MO, PRE), 6708 (MO); sandy alluvium near river at the entrance to the old Elandskloof Pass, *Goldblatt* 7122 (MO, PRE); Elandskloof, *Compton* 16748 (NBG).

33.19 (Worcester) Tulbagh Kloof to Piekenierskloof (AC), *Zeyher* 1647 (K, PRE, S); Tulbagh Kloof, *Compton* 12399 (NBG), *Ecklon & Zeyher Irid.* 23 (77.9) (MO, P, S); Gydo (AD), *Leipoldt* 3004 (BOL, K, PRE).

**2. *Moraea macrocarpa* Goldbl., sp. nov. TYPE:** South Africa. Cape: S of Redelinghuys, Picketberg district, *Acocks* 24359 (holotype, PRE; isotype, MO). FIGURE 6B.

Plantae 30–80 cm altae, ramis 1–3, cormo 8–12 mm diam., folio solitario tereti ad lineari-filiformi, spathis interioribus 4–5(–6.5) cm longis, exterioribus parvioribus, floribus caeruleis, tepalis exterioribus 2–3 cm longis, filamentis 5–6 mm longis, capsulis (18–)20–25 mm longis.

Plants 30–80 cm high, simple or few-branched.

*Corm* 8–12 mm diam.; tunics of fine pale fibers. *Leaf* solitary, canaliculate, terete to linear-filiform, 0.4–1.5 mm wide, erect, much longer than the spathes, inserted near, to well above the ground. *Stem* erect, filiform, simple or with two (to three) sessile or subsessile inflorescences. *Spathes* herbaceous, becoming dry above, the apices brown, acute, the inner (3.4–)4–5(–6.5) cm long, the outer about one-third as long as the inner. *Flower* blue-mauve, with yellow nectar guides, the claws of the outer tepals yellow with dark spots, scented; *outer tepals* 2–3 cm long, 7–10 mm at the widest, lanceolate; *inner tepals* 1.8–2.8 cm long, 5–7 mm wide, spreading. *Filaments* 5–6 mm long, united in the lower half; *anthers* 4–5 mm long, white. *Ovary* 17–21 mm long, included in the spathes, *style branches* 6–7 mm long, the crests linear-lanceolate, 12–18 mm long. *Capsule* cylindric, (18–)20–25 mm long. *Chromosome number*  $2n = 20$ .

*Flowering time.* (May–)August to early October; flowers opening soon after midday and fading at about 5 P.M.

*Distribution.* West coast from Hopefield to the Olifants River mouth and locally in the Breede River Valley, in deep white sand. Figure 1.

*Moraea macrocarpa* has been associated with *M. fugax* until now, or it has been confused with *M. filicaulis*, now *M. fugax* subsp. *filicaulis*. It bears a superficial resemblance to the latter in its slender stem, small corm, and small flower. Cytological study has, however, provided evidence that they are unrelated. *Moraea macrocarpa* has  $2n = 20$ , the basal diploid number for sect. *Subracemosae*, while *M. fugax* subsp. *filicaulis* has  $2n = 18$ , 12, and 10. The difference suggests that they may be derived from different ancestral stock, and the several differences between *M. macrocarpa* and *M. fugax* subsp. *filicaulis* are significant.

The differences between *Moraea macrocarpa* and *M. fugax* subsp. *filicaulis* include spathe, ovary and capsule length, and leaf number. The majority of specimens that I have examined of subsp. *filicaulis* have two leaves while *M. macrocarpa* has only one. The capsules of *M. macrocarpa*, its most striking attribute, are disproportionately long for the small plants and are in the 20–25 mm range. The ovary and the spathes are correspondingly long because the capsule remains enclosed in the spathes throughout development. The latter range from 4–6.5 mm long. In subsp. *filicaulis* the capsules are only 8–13



(–15) mm long and the spathes 2–3.5(–4) mm long. The flowering stem of subsp. *filicaulis* is typically branched, and the branches are usually distinctly stalked. In contrast the flowering stems of *M. macrocarpa* usually have only a single terminal inflorescence, rarely one to two branches, and the branches are more or less sessile.

*Moraea macrocarpa* occurs along the Cape west coast from Hopefield to Trawal in the Olifants River Valley and locally in the interior in the Breede River Valley near Worcester. It grows in deep, coarse-grained sand. Occasionally it occurs with the taller and more robust *M. fugax* subsp. *fugax*. Its range overlaps slightly that of *M. fugax* subsp. *filicaulis* in the Olifants River Valley but they have not been observed growing together.

*Specimens examined.* SOUTH AFRICA. CAPE: 31.18 (Vanhynsdorp) mountains W of Trawal, in sand (DC), Goldblatt 5661 (MO).

32.18 (Clanwilliam) 2 km N of the Lamberts Bay road towards Vredendal (AB), Nordenstam & Lundgren 1552 (MO, S); between Graafwater and Lamberts Bay (AB-BA), L. Bolus s.n. (BOL 23193); between Elandskloof and Clanwilliam (?BC), Leipoldt s.n. (BOL 20950); Alexandershoek (BD), Schlechter 5149 (BOL, GRA); 11.7 mi. S of Redelinghuys, white sand (DA), Acocks 24359 (MO, PRE); 9.5 mi. SW of Redelinghuys, Acocks 19689 (K); near Sauer, Piketberg (DD), Barker 2687 (NBG).

32.19 (Wuppertal) Pakhuis Pass (AA), Barker 1999 (NBG), Compton 9798 (NBG).

33.18 (Cape Town) Oosterwal, Hopefield (?AB), Pamphlett 89 (NBG); in planitie prope Darling (AD), H. Bolus 12833 (BOL, K).

33.19 (Worcester) Aan de Doorns, farm Reiers Rus, along the Breede River (CB), Goldblatt 6961 (MO, NBG).

**3. *Moraea fugax* (de la Roche) Jacq., Hort. Bot. Vindob. 3: 14. tab. 20. 1776; Goldblatt, J. S. African Bot. 36: 316. 1970; Ann. Missouri Bot. Gard. 63: 725. 1976 [1977]. *Vieusseuxia fugax* de la Roche, Descr. Pl. Aliq. Nov. 33. 1766. TYPE: Illustration in van Hazen, Cat. Arb. & Pl. 67. 1759 (lectotype designated by Goldblatt, 1970). FIGURE 7.**

(For additional synonyms see under the subspecies.)

Plants medium to large, 12–40(–50) cm high, branched. *Corm* (1–)1.5–3 cm diam.; tunics usually pale, rarely dark, of fine to medium fibers. *Cataphylls* usually two, membranous, pale, becoming dry and brownish and often broken above. *Leaf* solitary or two, equal or unequal in length, subopposite, inserted well above ground immediately below the first branch, canaliculate, usually much exceeding the stem and trailing,

occasionally loosely twisted distally. *Stem* erect or more often somewhat inclined, with a conspicuous, long lower internode, the branches crowded, occasionally subracemose. *Spathes* herbaceous, becoming dry, the upper margin light brown, apices attenuate; inner spathe (2–)2.5–6 (–8) cm long, the outer one-half to two-thirds as long as the inner. *Flowers* white, blue, or yellow, strongly scented; *tepals* lancolate, the limb more or less equal to the claw, the limb spreading horizontally or the inner occasionally erect, outer 2–4 cm long, inner 2–3.5 cm long, 5–8 mm wide. *Filaments* 5–10 mm long, united in the lower half; *anthers* 4–10 mm long. *Ovary* 8–20 mm long, included in the spathes, *style branches* 1.5–2 cm long, the crests lanceolate 6–18 mm long. *Capsule* oblong to cylindric, distinctly beaked, 9–28(–40) mm long. *Chromosome number*  $2n = 20, 18, 16, 14, 12, 10$ .

*Flowering time.* August to October, occasionally extending into December at high elevations.

*Distribution.* Northern Namaqualand to the southern Cape, typically in deep sandy or rocky sandstone or granitic soil. Figure 1.

As circumscribed here, *Moraea fugax* is an unusually variable species with several distinct forms or races. Of these only a series of dwarf, small-flowered and usually two-leaved populations, described in the past as separate species, *M. filicaulis* and *M. diphylla*, are given taxonomic recognition as subsp. *filicaulis*. This subspecies occurs throughout Namaqualand and extends south to the Clanwilliam district. Although subsp. *filicaulis* is itself somewhat variable, it appears to constitute a natural assemblage, united by its slender stem, filiform leaves, relatively small flower with tepals 2–2.6(–3.5) mm long and especially small capsules (10–15 mm long). Subspecies *filicaulis* apparently has  $x = 9$ . Some cytological variation is evident in karyotypes from several localities, and derived numbers of  $n = 6$  and 5 have been recorded.

The pattern of variation is more complex in subsp. *fugax*, the several forms of which are united by their large size, long broad leaves, and relatively large flowers with tepals 23–40 mm long and capsules 15–40 mm long. Chromosomal variation is particularly extensive in this subspecies with numbers ranging from  $2n = 20$  to 10. The variation within subsp. *fugax* is discussed in detail after the subspecies description.



## KEY TO THE SUBSPECIES

- 1a. Spathes short, 2–3.5(–4) cm long; capsules 9–13 rarely to 15 mm long; flowers small to medium, the outer tepals 2–2.6(–3.5) cm long; leaves filiform and usually two; branches clustered ..... 3B. subsp. *filicaulis*
- 1b. Spathes long, (3.5–)4–6.5 cm long; capsules 15–28(–40) mm long; flowers medium to large, the outer tepals 2.7–4 cm long; leaves channeled, linear, either one or two; branches usually clustered but sometimes subracemose ..... 3A. subsp. *fugax*

**3A. *M. fugax* subsp. *fugax*. FIGURE 7A.**

*Iris edulis* L. f., Suppl. Pl. 93. 1781; *Moraea edulis* (L. f.) Ker, Bot. Mag. 17: tab. 613. 1803; Baker, Fl. Cap. 6: 20. 1896; *Vieusseuxia edulis* (L. f.) Link, Enum. Hort. Berol. Alt. 1: 56. 1821. TYPE: South Africa. Cape: exact locality uncertain, *Thunberg s.n.* [lectotype, Herb. Thunb. 1123 (UPS), designated by Goldblatt, 1976b].

*Moraea corniculata* Lam., Tabl. Encycl. 1: 114. 1791; Encycl. 4: 227. 1797. TYPE: South Africa. Cape, *Sonnerat s.n.* (lectotype, P, designated by Goldblatt, 1976b).

*Iris longifolia* Schneev., Icon. Pl. Rar. 7: tab. 20. 1792; *Moraea longifolia* (Schneev.) Sweet, Hort. Brit., ed. 2, 496. 1830, nom. illeg., non *M. longifolia* (Jacq) Pers. (1805). TYPE: South Africa. Cape: without precise locality (lectotype, illustration in Schneev., Icon. Pl. Rar. 7: tab. 20. 1792, designated by Goldblatt, 1976b).

*Moraea odora* Salisb., Parad. Lond. 1: tab. 10. 1805. TYPE: Illustration in Salisb., Parad. Lond. 1: tab. 10. 1805 (lectotype designated by Goldblatt, 1976b).

Plants medium to large, 12–40(–50) cm high, branched. *Corm* (1–)1.5–3 cm diam.; tunics usually pale, rarely dark, of fine to medium fibers. *Leaf* usually solitary, occasionally two, equal or unequal in length, canaliculate, usually much exceeding the stem and trailing. *Stem* sturdy, 2–3 mm thick. *Inner spathe* 4–8 cm long, the outer ca. one-third the length of the inner. *Flowers* white, blue, or yellow, strongly scented; *outer tepals* 2.3–4 cm long, lanceolate, the limb more or less equal the claw; *inner tepals* 2–3.5 cm long, erect or slight reflexed, 5–8 mm wide. *Filaments* 6–10 mm long; *anthers* 4–8 mm long. *Ovary* 14–20 mm long, *style branches* 1.5–2 cm long, the crests lanceolate, 10–18 mm long. *Capsule* clavate to cylindrical, distinctly beaked, 1.5–2.8(–4) cm long; *seeds* many, angled. *Chromosome number*  $2n = 20, 18, 16, 14, 12, 10$ .

*Flowering time.* August to November, extending into December at higher elevations.

*Distribution.* Namaqualand to the southern

Cape, frequently in sandy situations. Figures 1, 3, 4.

*Variation.* Plants corresponding to the type of *Moraea fugax* have large, yellow flowers, a single leaf, and are of generally moderate size with an umbellate branching pattern (although tall racemosely branching plants may occur). Populations of this form occur in the south of the range of subsp. *fugax* and extend from south of Malmesbury to the Cape Peninsula and east to Robertson and Swellendam. The most frequent karyotype (Fig. 4) has  $n = 5$ , but in the east of its range, at Swarttrivier, north of Caledon Zwartberg, plants have  $n = 7$ . Similar but more slender yellow-flowered populations in the interior near Robertson and to the north in the Cedarberg at Brandewyn River and Algeria have  $n = 9$ , and a population in Pakhuis Pass has  $n = 8$ . Despite this range of karyotypes, there seem to be no morphological features that distinguish the cytotypes. A yellow-flowered form from the Olifants River Valley and adjacent valleys is similar to yellow-flowered plants that occur to the south except that they consistently have erect inner tepals. These plants also have  $n = 5$  but have a somewhat different karyotype from the southern form that has the same number.

A second form that occurs in the southern part of the range of subsp. *fugax* has deep blue flowers, is relatively tall, and is late blooming. On the Cape Peninsula and the Cape Flats the yellow-flowered form, described above, blooms in August and September, while the blue-flowered form blooms only in October or later, and flowering plants have been collected as late as January. Populations of this form usually have  $n = 6$ , but  $n = 7$  was found in a population near Cape Point. This form is not well sampled.

Along the west coast from near Malmesbury as far north as Hondeklipbaai in Namaqualand (Fig. 3), there is a large, white-flowered form of the species corresponding to Baker's *Moraea edulis* var. *longifolia*. It is generally tall and racemosely branched. This robust form also occurs in the Olifants River Valley. Most populations have  $n = 10$  or 9, but  $n = 7$  and 6 are found in the Velddrif and Hopefield areas (Goldblatt, 1971: 348; Fig. 2E).

In the Malmesbury district there is a distinctive white-flowered form that has relatively large flowers with unusually narrow tepals. Populations around Malmesbury and to the north towards Hopefield have  $n = 8$ , but plants corre-





FIGURE 7. Morphology of *Moraea fugax*.—A. Subsp. *fugax*, large white-flowered form.—B. Subsp. *filicaulis*. Habits  $\times 0.5$ ; flowers life size.

sponding to this form from south near Gouda have  $n = 6$ . In the Breede River Valley similar plants have  $n = 9$  (Fig. 3).

There is no recorded intrapopulational vari-

ation for flower color. Occasionally there is a trend for white flowers to be replaced gradually over some distance by blue ones as in the Picketberg district. In the Olifants River Valley pop-



ulations of white- or yellow-flowered plants alternate over distances of several kilometers without any clear pattern. The yellow-flowered populations consistently differ in having erect inner tepals and as far as is known,  $n = 5$ .

**History.** *Moraea fugax* is typified by an illustration of a yellow-flowered plant of unknown origin, most probably collected on or near the Cape Peninsula. It was cultivated in Holland in the mid-seventeenth century and figured in the 1759 "Catalogue des Arbores et Plantes" of the van Hazen, Vakinburg & Company Nursery. The plant was described by Daniel de la Roche in 1766 and the illustration in van Hazen's Catalogue is assumed to be the type. *Moraea fugax* was first assigned to the genus *Vieusseuxia* but was transferred to *Moraea* by Jacquin in 1776, who figured the blue-purple-flowered form of subsp. *fugax* but considered it conspecific with plants with yellow flowers. Subsequently, other forms of subsp. *fugax* were described from plants in cultivation in Europe, notably *M. longifolia* (as *Iris*) by Schneevoegt in 1792 and *M. odora* by Salisbury in 1805. Both these species represent the robust white-flowered form of subsp. *fugax*.

**Specimens examined.** SOUTH AFRICA. CAPE: 29.17 (Springbok) Komaggas (CD), *Maguire* 403 (NBG).

30.17 (Hondekliptbaai) near Soebatsfontein (BA), *van Berkel* 268 (NBG).

30.18 (Kamiesberg) Eenkokerboom, in collibus' (CC), *Schlechter* 11063 (MO, P).

31.18 (Van Rhynsdorp) Vredendal commonage (CB-DA), *Hall* 3844 (NBG, PRE, STE), *Bayliss* 6126 (MO); Nardouw Pass, *Lewis s.n.* (BOL-22205); top of Gifberg (DC), *Bayliss* 6161 (MO); W of Klawer, below the Winterhoekberg, *Goldblatt* 5778 (MO); slope above the Olifants River at the bridge near Klawer, *Goldblatt* 2828 (MO); 5 km S of Trawal, Olifants River Valley, *Goldblatt* 5792 (MO); hills W of Trawal on the road to Kleipan, *Goldblatt* 5667 (MO).

31.19 (Calvinia) sandy places near Nieuwoudtville (AC), *Galpin* 11128 (K, PRE); near Nieuwoudtville, *Buhr s.n.* (Nat. Bot. Gard. 639/29 in BOL), *Goldblatt* 5843 (MO); Doornbosch (CC), *Hall* 3881 (NBG, STE); top of Botterkloof (CD), *van Niekerk* 3197 (BOL), *Hall* 3876 (NBG); farm Soutpan, ca. 42 km SE of Nieuwoudtville, *Goldblatt* 7080 (MO).

32.18 (Clanwilliam) sandy slope N of Clanwilliam facing the Olifants River (BB), *Goldblatt* 5936 (MO); between Clanwilliam and Graafwater, *Goldblatt* 5161 (MO); sandveld near Velddrif (CC), *van Jaarsveld s.n.* (MO); hills NW of Moutons Vlei (DC), *Pillans* 7398 (BOL); Piketberg (DD), *Compton* 22989 (NBG), *H. Bolus s.n.* (MO); N of Piketberg towards Piekenierskloof, *Goldblatt* 5676 (MO).

32.19 (Wuppertal) Cedarberg Pass near Algeria (AC), *Goldblatt* 3250 (MO); Cedarberg at Algeria, *Viviers s.n.* (MO).

33.18 (Cape Town) Langebaan (AA), *Lewis s.n.* (BOL); between Hopefield and Langebaan, *L. Bolus s.n.* (BOL-20339, K); near Hopefield, *Marloth* 8207 (PRE); Groenekloof (AD), *Zeyher* 1646 (K, PRE, S); road to Bokbaai, *Goldblatt* 5850 (MO); 20 km NW of Malmesbury on the road to Hopefield (BB), *Goldblatt* 4081 (MO); Malmesbury (BC), *Barker* 2554 (NBG), *Goldblatt* 4813 (MO); 8 km N of Malmesbury, *Goldblatt* 3025 (MO, NBG, PRE); sandy slopes S of Malmesbury opposite Abbotsdale, *Goldblatt* 5116 (MO); slopes of Koeberg N of Cape Town (DA), *Goldblatt* 4080 (MO); near Sea Point, Cape Town (CD), *Wolley Dod* 1611 (BOL); Wynberg Hill, *Pillans* 1950 (MO); Kirstenbosch, *Barker* 2066 (BOL), *Verdoorn s.n.* (PRE); Table Mountain, *Ecklon* 823 (PRE-11149).

33.19 (Worcester) hills near Saron (AA), *Schlechter* 10605 (BR, K, MO, PRE, S); foot of the Elandsrivier Mts. on the farm Elandsberg (AC), *Goldblatt* 5851 (MO); Michells Pass (AD), *Schlechter* 8966 (GRA); Aan de Doorns, farm Reiers Rus, near Moordkuil (CB), *Goldblatt & Snijman* 6962 (MO); near French Hoek (CC), *Gillett* 1830, 1831 (STE); 15 km from MacGregor on Bonnievale road (DD), *Marsh* 806 (PRE, STE); hills above Goree, S of the Robertson-Ashton road, *Goldblatt* 5860 (MO).

34.18 (Simonstown) beyond Simonstown (AB), *Wolley Dod* 505 (BOL, K); Fish Hoek, *Wolley Dod* 1633 (BOL, K); burned lower slopes of Klaasjagersberg, opposite Cape Point Reserve, *Goldblatt* 5264 (MO); Silvermine road just N of the Noordhoek turnoff, *Goldblatt* 5154 (MO); Olifants Bos (AD), *Barker* 3876 (BOL, NBG); Smitswinkel, Cape Peninsula, *Walgate* 433 (NBG); Cape Reserve, S of Sirkels Vlei, *Goldblatt* 5403 (MO); Strandfontein (BA), *Rycroft* 2371 (MO); dunes near Strand (BB), *Parker* 4141 (BOL, K).

34.19 (Caledon) burned flats at the foot of Houw Hoek Pass (AA), *Goldblatt* 4292 (MO); Caledon (AB), *Gillett* 1111 (STE); N side of Caledon Swartberg, *Goldblatt* 5782 (MO); Onrust River (AC), *Van Niekerk* 300 (BOL); Mainstay, Onrus River, *Robertson* 111 (MO); roadside ca. 10 km S of Bot River, *Goldblatt* 2997 (MO); Die Duine, Hermanus, stabilized sand dunes, 50 m (AD), *Williams* 1010 (MO, PRE, US, WAG).

34.20 (Bredasdorp) near Storms Vlei (AA), *Goldblatt* 2923 (MO, PRE); 14 km E of Swellendam (BA), *Story* 3090 (PRE); Cape Infanta (BD), *Blum* 64 (E), 214 (E); Zoetendals Vlei (CA), *Leipoldt* 3559 (PRE).

34.21 (Riversdale) Riversdale (AB), *H. Bolus s.n.* (BOL).

34.22 (Mossel Bay) Mossel Bay (AA), *Burchell* 6295 (K); Ruigte Vlei, near Knysna (BB), *Fourcade* 1557 (BOL, GRA).

WITHOUT PRECISE LOCALITY: 'Clanwilliam, am Fluss Olifantrivier und bei Villa Brakfontein' *Ecklon & Zeyher Irid.* 16 (76.10) (MO); 'Worcester, Tulbaghskloof, Tulbaghsthal, am Fuss des Winterhoeksberg' etc., *Ecklon & Zeyher Irid.* 23 (77.11) (MO); 'bei Puspasvlei, Voormansbosch, Duiwelsbosch' etc., *Zeyher* 4079 (70.10) (S).

**3B. *M. fugax* subsp. *filicaulis* (Baker) Goldbl., stat. nov. *Moraea filicaulis* Baker, Handb. Irid. 56. 1892. TYPE: South Africa. Cape: Kamiesberg between Roodeberg and Ezel-**



skop, *Drège* 2605 (lectotype, K, designated by Goldblatt, 1976b; isoelectotypes, MO, P). FIGURE 7B.

*Moraea diphylla* Baker, Bull. Misc. Inform. 1906: 42. 1906. TYPE: South Africa. Cape: Olifants River, *Penther* 734 (lectotype, K, designated by Goldblatt, 1976b).

Plants small to medium, 6–12(–20) cm high, few to several-branched. *Corm* 7–16 mm diam.; tunics usually pale, rarely dark, of fine to medium fibers. *Leaves* usually two and subopposite, occasionally solitary, linear-filiform, channeled, 1–2 mm wide, equal or occasionally unequal in length, occasionally loosely spiraled distally. *Stem* slender, to 1 mm thick. *Inner spathe* 2–3.5(–4) cm long, the outer half to one-third as long as the inner. *Flowers* white, sometimes shaded bluish or pinkish, rarely dark blue-violet, scented, with yellow nectar guides; *tepals* lanceolate, limbs spreading horizontally, outer 2–2.6(–3.5) cm long, 0.8–1.2 mm wide; inner 1.8–3 cm long, 5–7 mm wide. *Filaments* 5–6 mm long; *anthers* 4–5(–6) mm long. Ovary 8–10 mm long, the *style branches* 8–10 mm long, the crests lanceolate 8–14 mm long. *Capsule* 10–13(–15) mm long. *Chromosome number*  $2n = 18, 12, 10$ .

*Flowering time.* August to October.

*Distribution.* Namaqualand south to the Olifants River Valley near Clanwilliam, in sandy or rocky soil. Figure 5.

*Moraea fugax* subsp. *filicaulis* is a small-flowered subspecies with a slender stem, small corm, and usually two filiform leaves. The subspecies ranges from northern Namaqualand to the central Olifants River Valley near Clanwilliam (Fig. 5). There are three chromosome numbers recorded in the taxon,  $n = 9$  in one population,  $n = 6$  in three populations, and  $n = 5$  in two populations. The type form of *M. filicaulis*, from the Kamiesberg, has deep blue-purple flowers and  $n = 6$ , the karyotype having a conspicuous long acrocentric chromosome pair with a large terminal satellite. White-flowered plants from near Kamieskroon, matching the type of the synonym, *M. diphylla*, have an identical karyotype. Plants from the type area of *M. diphylla* in the Clanwilliam district, also white-flowered, have either  $n = 9$  or 5, the latter karyotype with one long metacentric and five acrocentric pairs. A similar karyotype occurs in plants with somewhat larger flowers from northern Namaqualand. A population from the Richtersveld at the extreme of the range of the subspecies has  $n =$

6 and a comparable karyotype in which one very small metacentric chromosome pair stands out. There is probably more variation in the subspecies yet to be recorded, and it is premature to attempt to construct a hypothetical pattern of chromosome evolution for subsp. *filicaulis*. Available data suggest that  $n = 9$  is the ancestral number.

*Specimens examined.* SOUTH AFRICA. CAPE: 29.17 (Springbok) Richtersveld, Eksteenfontein road 3–4 km N of the Port Nolloth–Steinkopf road (AB), *Goldblatt* 5717 (MO, PRE); Spektakelberg (DA), *Barker* 1340 (NBG), 7423 (NBG); near Okiep (DB), *H. Bolus* 6616 (BOL); hills above Okiep, *Marloth* 9880 (PRE); Springbok, *Esterhuysen* 5879 (BOL); Blou Stasie, near Springbok, *Leighton* 1173A (BOL); sandy flats below Wildeperdehoek Pass (DC), *Goldblatt* 5761 (MO); 21 km SW of Springbok (DD), *Acocks* 19576 (K, PRE).

30.17 (Hondeklipbaai) granite hills 2 km N of Kamieskroon (BB), *Goldblatt* 4254 (MO); Kamieskroon, *Lewis* 5478 (NBG); 14 km NNW of Garies (BD), *Acocks* 14964 (PRE); Buffels River to Soebatsfontein, *Leighton* 1211 (BOL); Brakdam hills, *Schlechter* 11111 (BOL).

30.18 (Kamiesberg) Kamiesberg, E slopes Rooiberg (AC), *Goldblatt* 4308 (MO); sandy field below Studers Pass, *Goldblatt* 635 (BOL); Kamiesberg between Rooiberg and Ezelskop, *Drège* 2605 (K, MO, P); Koms Ravine (CA), *Pearson* 6665 (K); between Bitterfontein and Garies (CA-CC), *Pillans* 6346 (BOL), *Leipoldt* 3846 (BOL).

31.18 (Vanrhynsdorp) 1 km N of farm Komkans, Kliphuis se Kop (AA), *Nordenstam & Lundgren* 1710 (MO, NBG, S); 4 mi. N of farm Komkans, Geelkop, *Nordenstam & Lundgren* 1720 (MO, S); Van Rhynsdorp (DA), *Barker* 3642 (NBG); Vredendal Commonage, *Hall* 3843 (NBG, PRE, STE); 10 km N of Van Rhynsdorp, *Acocks* 19499 (M, NBG, PRE); N slopes of Gifberg (DC), *Goldblatt* 207 (BOL); hills W of Trawal on the Kleipan road, *Goldblatt* 5666 (MO).

32.18 (Clanwilliam) Lamberts Bay (AB), *Henrici* 3300 (PRE); near Olifants River at Clanwilliam (BB), *Penther* 734 (K); Ramskop, Clanwilliam, *Goldblatt* 7376 (MO).

WITHOUT PRECISE LOCALITY: Richtersveld, *Marloth* 12207 (BOL); Querung des Olifantsrivier, *Penther* 554 (BOL); Namaqualand Minor, *Scully* 111 (BOL).

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